Variation in body condition of songbirds during breeding season in relation to sex, migration strategy and weather

Andersson, Noora

2018

Andersson , N , Piha , M , Meller , K , Välimäki , K & Lehikoinen , A 2018 , ' Variation in body condition of songbirds during breeding season in relation to sex, migration strategy and weather ' , Ornis Fennica , vol. 95 , no. 2 , pp. 70-81 .

http://hdl.handle.net/10138/250887

unspecified
publishedVersion

Ornis Fennica 95: 70–81. 2018

Variation in body condition of songbirds during breeding season in relation to sex, migration strategy and weather

Noora Andersson, Markus Piha, Kalle Meller, Kaisa Välimäki & Aleksi Lehikoinen*

*N. Andersson, M. Piha, K. Meller, K. Välimäki, A. Lehikoinen, Finnish Museum of Natural History, P.O. Box 17,FI-00014 University of Helsinki, Finland. * Corresponding author's e-mail: aleksi.lehikoinen@helsinki.fi*
K. Välimäki, Jyväskylä Center for Interdisciplinary Brain Research, P.O. Box 35, FI-40014 University of Jyväskylä, Finland

Received 6 December 2017, accepted 23 May 2018

Animal body reserves are often linked with demographic parameters such as breeding success and survival. During breeding season individuals face a trade-off between maintaining body reserves and investing in reproduction. Factors influencing the body reserves of species during breeding season are poorly understood. In this study, we used long-term trapping data from Finnish Constant Effort Sites program to evaluate the impact of sex, migration behaviour, and weather on body reserve index (BRI) of old and young birds during breeding season in 20 species. Our main interest was to study how variation in weather conditions influences the BRI of breeding passerine birds. Weather variables did not explain BRI of adults. However, we found that BRI of young birds was weakly negatively connected with mean temperature, but this may have low biological importance. BRI of adult males increased towards the end of August, but female BRI showed a seasonal decline throughout June and July. Breeding females face the peak in physiological stress later than males, probably because females lay eggs, and often invest more in incubation and brood rearing than males. The seasonal decline caused females to have lower BRI than males at the end of the breeding season. This can cause females to be less prepared for the approaching autumn migration than males. Our findings suggest that there are sex-specific changes in BRI during the breeding season, which may have carry-over effects on other life history events.

1. Introduction

The body reserves (typically measured as mass corrected for size) of animals are often linked with demographic parameters, such as breeding success and survival (Hamer *et al*. 1993, Ebbinge & Spaans 1995, Morrison *et al*. 2007). Higher body reserves have been found to improve breeding success in e.g., birds, fish and mammals (Gaillard *et al*. 1992, Pietiäinen & Kolunen 1993, Lindström 1998, Fujii *et al*. 2005, Jacobs *et al*. 2013). Furthermore, winter survival has been shown to increase with increased body reserves (Duriez *et al*. 2012). On the other hand, high fat reserves may elevate predation risk (Houston & McNamara 1993). During the breeding season, individuals face a trade-off between their own body condition and reproductive investment (Mitchell *et al*.

VERTAISARVIOITU
KOLLEGIALT GRANSKAD
PEER-REVIEWED
www.tsv.fi/tunnus

2012). It is also widely known that weather conditions during the brood rearing period can influence breeding success (Kostrzewa & Kostrzewa 1990, Ludwig *et al*. 2006, Lehikoinen *et al*. 2009). Weather conditions may also affect the body reserves and survival of individuals after the brood rearing period (Vernasco *et al*. 2018). While the general variation of body condition during a breeding season is fairly well known in some commonly studied species (Hillström 1995, Merilä & Wiggins 1997, Moe *et al*. 2002), the contribution of weather conditions on body reserves of breeding species throughout the reproductive season has been less well characterized. Understanding how the weather affects the body condition of species is important, since poor post-breeding weather conditions may have long lasting carry-over effects (Ebbinge & Spaans 1995, Duriez *et al*. 2012).

Weather conditions can influence body reserves in several ways. Increased precipitation, for example, raised the amount of earthworms in the summer diet of Song Thrushes *Turdus philomelos* leading to increase in body reserves (Gruar *et al*. 2003). Drought has been connected with poor body reserves of adult and young Townsend's ground squirrels (Van Horne *et al*. 1997), and rainfall can also have negative impact on the breeding success of species and body condition and growth rate of young (Kostrzewa & Kostrzewa 1990, Bradbury *et al*. 2003, Lehikoinen *et al*. 2009, Chausson *et al*. 2014, Pérez *et al.* 2016). Moreover, the effect of weather on body reserves may be age dependent (Smith & Jenkins 1997). The impact of weather can also be dependent on the length of the time period when an animal is exposed to harsher climatic conditions, and the relevant time-period can vary from a single day to several weeks (Ludwig *et al*. 2006, Lehikoinen *et al*. 2009, Chausson *et al*. 2014).

The aim of this paper is to investigate how weather variables and the timing of the breeding season influence the body reserve index (BRI, index of ratio between body mass and wing length) of passerine birds of different sex, age and migration strategy. We expect that BRI correlates negatively with the amount of rainfall, as rain can hamper the availability of insects, which are the main food source to most of the species investigated here (Bradbury *et al*. 2003, Pearce-Higgins *et al*. 2015). For temperature effects we have two competing hypotheses. First, as our study site is located in the cold boreal zone, we expect that higher temperature would increase the body condition of individuals because cold temperatures can decrease insect availability (Møller 2013), and increase the use of body reserves due to higher metabolic rate (Castro *et al*. 1992, Krams *et al*. 2013).

Alternatively, birds may accumulate body reserves during colder periods to tolerate harsher conditions, i.e., actively optimize their body condition (Rogers 1995, Klaassen *et al*. 2004). Increased temperature may thus be associated with lower body condition since relatively lighter body could be beneficial for predator avoidance (Houston & McNamara 1993, Bond & Esler 2006, Esler & Bond 2010). Body mass of small-sized passerines can change several percents in a day depending on rate of food intake (Macleod *et al*. 2005; Bauchinger *et al*. 2011), thus weather dependent resource availability may influence body resources of study species in a relatively short period of time. Here we examined the impacts using the weather variables within a week, which should be a period long enough to cause decrease in body reserves if conditions are unfavourable (Bauchinger *et al*. 2011). Responses to weather can also be age and sex dependent.

We predict that BRI is dependent on sex among breeding adults. Females often invest more to breeding than males (Hemborg 1999), which may cause larger variation in their BRI. Females may have lower BRI during brood rearing than males, which invest in mate attraction and defence of a territory in the early phase of breeding, but do not lay eggs, and generally invest less in the feeding of chicks (Hemborg 1999). Body resources are typically increasing for the migration period (Alerstam 1990, Newton 2008, Zaniewicz *et al*. 2018). We hypothesize that male BRI show stable or increasing trend towards the end of the breeding season as males may start gathering resources for autumn migration earlier than females. Females on the other hand are predicted to show U-shape changes in BRI: BRI is likely high during egg laying and incubation (beginning of the study period) and decrease during brood rearing period in the middle of the study period, and BRI starts to increase before the approaching autumn migration at the end of the period. However, larger investments

Table 1. Migration behaviour (SDM or LDM, short- or long-distance migrant, respectively) and sample sizes of the study species separated for adult males, adult females and young including both first encounter birds and recaptures, see methods).

Species	Scientific name	Migration	Adult males	Adult females	Young
European Robin	*Erithacus rubecula*	SDM	226	276	6,112
Redwing	*Turdus iliacus*	SDM	185	182	514
Common Blackbird	*Turdus merula*	SDM	254	164	470
Fieldfare	*Turdus pilaris*	SDM	262	238	381
Blue Tit	*Cyanistes caeruleus*	SDM	268	377	2,452
Great Tit	*Parus major*	SDM	535	557	3,128
Common Chaffinch	*Frincilla coelebs*	SDM	570	641	728
European Greenfinch	*Carduelis chloris*	SDM	277	183	437
Eurasian Siskin	*Carduelis spinus*	SDM	356	198	886
Reed Bunting	*Emberiza schoeniclus*	SDM	651	647	1,908
Thrush Nightingale	*Luscinia luscinia*	LDM	241	164	289
Eurasian Blackcap*	*Sylvia atricapilla*	LDM	148	164	700
Garden Warbler	*Sylvia borin*	LDM	377	795	1,596
Common Whitethroat	*Sylvia communis*	LDM	523	452	1,844
Lesser Whitethroat	*Sylvia curruca*	LDM	46	111	1,361
Sedge Warbler	*Acrocephalus schoenobaenus*	LDM	2,180	1,519	5,627
Reed Warbler	*Acrocephalus scirpaceus*	LDM	200	138	831
Willow Warbler	*Phylloscopus trochilus*	LDM	1,030	1,028	7,674
European Pied Flycatcher	*Ficedula hypoleuca*	LDM	824	626	1,121
Common Rosefinch	*Carpodacus erythrinus*	LDM	460	293	322

* In large parts of Europe Blackcap is a SDM, but in Finland majority of the population winters in Africa arriving in May and early June (see Valkama *et al*. 2014).

in the breeding among females may delay their ability to increase their BRI before autumn migration.

Since migration strategy may influence variation in BRI, we compared two functional groups: long-distance and short-distance migrants (including partial migrants); hereafter LDM and SDM, respectively. The majority of long distance migrants are insectivorous, which is why they need to migrate to the tropical areas for the winter (Alerstam 1990). Because of their diet, they could be more vulnerable to changes in weather as cold weather, for instance, may hamper insect availability (Møller 2013).

Therefore, we expect LDMs show stronger responses to weather conditions than short distance migrants and partial migrants. Migratory behaviour may also influence seasonal changes in BRI. LDMs are more likely to be constrained by the short breeding season, as they arrive later, start breeding later and depart earlier from the breeding grounds than SDMs (Lehikoinen 2011, Kluen *et al*. 2017), whereas SDMs have longer breeding season (sometimes with multiple broods) and depart typically later than LDMs (Newton 2008, Lehikoinen 2011). We expect that LDMs should show faster increase in BRI towards the end of the breeding season when birds are preparing for autumn migration (Newton 2008). Among young, we expect increasing BRI towards the end of the season, which is faster among LDMs as they depart earlier than SDMs.

2. Material and methods

2.1. Constant Effort Sites Data

We used bird-ringing data based on standardized mist netting from 178 different sites belonging to the constant effort sites (CES) project in Finland (Piha 2014, Meller *et al*. 2016). The data was collected during the years 1986–2014 between May and August, and on average 33 sites participated in the project annually (Piha 2014). Altogether 141 volunteer ringers have participated in the collection of the data. This study focused on 20 most

abundant CES species (listed in Table 1) with 67,832 observations from 61,651 individuals including both wing length (maximum chord; Svensson 1992) and body mass measures. Bird species were classified into SDMs (wintering in Europe or Mediterranean region including partial migrants; there are no abundant clearly resident species in CES) and LDMs (wintering in tropical areas) based on Valkama *et al*. (2014). The SDM group consisted of 27,355 observations from 24,776 individuals, and the LDM group consisted of 40,477 observations from 36,565 individuals.

Each observation included ringing or recovery date, bird ID (ring number), site ID, ringer ID, bird species, age (young = born during the same year, adult = born during previous breeding season or earlier), sex (when determined; (Svensson 1992)), weight, wing length (maximum chord measurement, as described by Svensson 1992), and coordinates of the ringing or recovery site. Nestlings, fledglings and fatally injured individuals as well as individuals with ambiguous ring id, species- or age information, were excluded from the data. The sex was used as a variable only in adult birds (hereafter male and female equal to adult male and adult female, respectively).

For individuals with more than one observation, the consistency of sexing was examined. In case of inconsistencies, observations were left out from the analyses. We included moulting individuals only if there was another record of the bird with fully grown wing. The data included observations from 1 June to 31 August, and 16 June to 31 August for adults and young birds, respectively, as the number of observations of young individuals in Finland in early June is low or negligent for the majority of species in the LDM group. For every species, only the observations from ringers with > 9 ringings of that species were included in the analyses. We did not consider time of the day in the analyses because the trapping period was similar through the season, although this may have added more unexplained noise to the analyses.

2.2. Weather data

The daily mean temperature and the sum of daily rainfall for each CES location were extracted from a data provided by The Finnish Meteorological Institute, in which observations from c. 100 weather stations have been interpolated into 10 x 10 km grid cells (Venäläinen *et al.* 2005). To assess the short-term effects of local weather conditions on body condition, the sum of rainfall and mean temperature were calculated for seven days prior to capture date of each observation from the particular site.

2.3. Statistical Analysis

Body reserve index was computed as the standardized residuals of the regression of log(mass) on log(wing length) (Ormerod & Tyler 1990, Öst *et al.* 2003). The calculation was done species-by-species and residuals were standardized (mean zero, standard deviation 1) before the analyses.

We used linear mixed models to analyze the effect of weather conditions on body reserves using BRI as response variable. We conducted analyses separately for adults and young, as young birds often cannot be sexed in the field, and the breeding investments of adults may cause different patterns between age groups.

Among adults, fixed effect variables (explanatory variables) included migration behaviour, sex, date (as day of year, linear and quadratic effect), temperature and rainfall. Random effect variables included site, year, ringer and species, all modelled as random intercepts. Site was included into the model to rectify for the potential spatial variability in body condition as e.g. body size of species tend to increase towards the poles (so called Bergmann's rule; Bergmann 1847, Brommer *et al.* 2014), and year was added to account for the potential differences between years. Ringer ID was included to account for potential differences in the measurements.

Species was included since the wing length and body mass proportions naturally vary between bird species. We used only the last observation of each individual in the analyses, as recaptures were relatively rare (17.5% and 4.2% of all trappings were recaptures among adults [n = 27,634 trappings altogether] and young [n = 40,198]) and use of individual ID as a random factor was thus not used. The last observation of the individual was selected to increase the sample sizes in the second half of the study period especially in adults (see Fig. 1). We built eight models explaining BRI of

Table 2. Models explaining variation of body reserve index in adult birds of 20 passerine species during breeding season. AIC difference (Δ*AIC*), number of parameters (*K*) and AIC weights (*w*) are given. Mig is migratory behaviour, Sex is the sex of the individual, Date is the calendar day, T and R are the mean temperature and the sum of rainfall during seven days before the trapping of the bird.

Model	Δ*AIC*	*K*	*w*
Mig+Sex+T+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Mig*T+Sex*T +Sex*Date+Sex*Date^2+ Sex*Mig*Date+Sex*Mig*Date^2	0.00	25	0.473
Mig+Sex+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Sex*Date+Sex*Date^2 +Sex*Mig*Date+Sex*Mig*Date^2	0.21	22	0.427
Mig+Sex+R+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Mig*R+Sex*R +Sex*Date+Sex*Date^2+ Sex*Mig*Date+Sex*Mig*Date^2	4.11	25	0.061
Mig+Sex+T+R+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Mig*T+Sex*T +Mig*R+Sex*R+Sex*Date+ Sex*Date^2+ Sex*Mig*Date+Sex*Mig*Date^2	4.98	28	0.039
Mig+Sex+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Sex*Date+Sex*Date^2	248.92	19	0.000
Mig+Sex+T+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Mig*T+Sex*T +Sex*Date+Sex*Date^2	250.71	22	0.000
Mig+Sex+R+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Mig*R+Sex*R +Sex*Date+Sex*Date^2	251.96	22	0.000
Mig+Sex+T+R+Date+Date^2+Mig*Date+Mig*Date^2+Mig*Sex+Mig*T+Sex*T +Mig*R+Sex*R+Sex*Date+ Sex*Date^2	254.92	25	0.000
Mig+Sex+Date+Date^2	1211.28	10	0.000

Table 3. Models explaining variation of body reserve index in young birds of 20 passerine species during breeding season. AIC (Δ*AIC*) difference, number of parameters (*K*) and AIC weights (*w*) are given. Mig is migratory behaviour, Sex is the sex of the individual, Date is the calendar day, T and R are the mean temperature and the sum of rainfall during seven days before the trapping of the bird.

Model	Δ*AIC*	*K*	*w*
Mig+T+Date+Date^2+Mig*T+Mig*Date+Mig*Date^2	0.00	18	0.578
Mig+T+R+Date+Date^2+Mig*T+Mig*R+Mig*Date+Mig*Date^2	1.06	20	0.340
Mig+Date+Date^2+Mig*Date+Mig*Date^2	4.36	16	0.065
Mig+Date+Date^2	5.49	14	0.036
Mig+R+Date+Date^2+Mig*R+Mig*Date+Mig*Date^2	6.99	18	0.018

adults (Table 2), where the most complicated model included following fixed effects

BRI = Mig + Sex + T + R + Date + Date^2 + Mig*Date + Mig*Date^2 + Mig*Sex + Mig*T + Sex*T + Mig*R + Sex*R + Sex*Date + Sex*Date^2 + Sex*Mig*Date + Sex*Mig*Date^2 (1)

where, Mig is migration behaviour, Sex is the sex of the individual, T is temperature, R is rainfall, Date is calendar day. Furthermore, random factors included location of the trapping site, trapping year, ringer who has taken the measurements and the calendar day nested for study species to allow species specific seasonal changes.

Among young birds, we had five model combinations (Table 3), where the most complicated model was

BRI = Mig + T + R + Date + Date^2 + Mig*T + Mig*R + Mig*Date + Mig*Date^2 (2)

where Mig is migration behaviour, T is temperature, R is rainfall, Date is calendar day. The random factors were the same as in the models of adults. Continuous variables (date and weather variables) were standardized before the analyses (mean 0, standard deviation 1). Competing models were ranked based on AIC and in case of several equally good models, we used model averaging (Burnham & Anderson 2002).

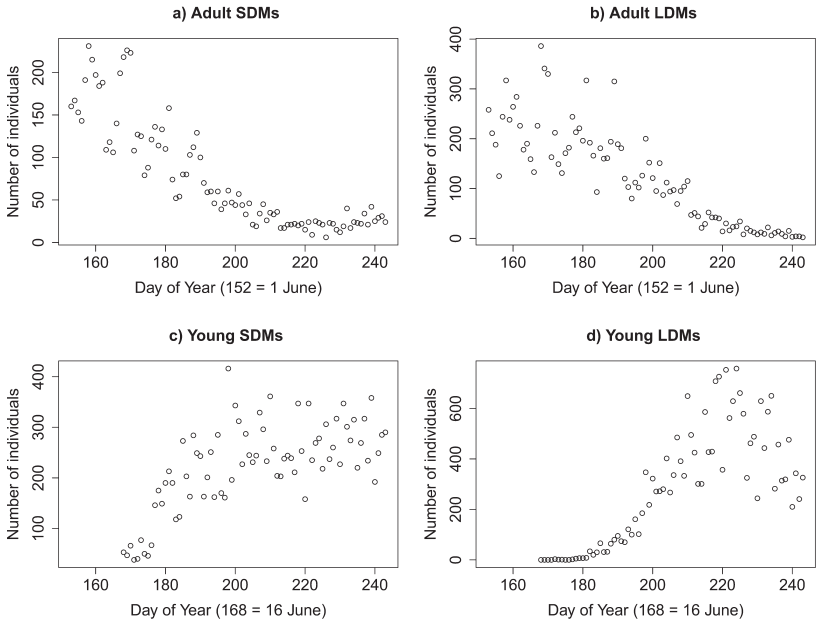

Fig. 1. Calendar day sample sizes of a) adult SDMs (short-distance migrants) and b) adult LDMs (long-distance migrants), c) young SDMs and d) young LDM during the study period (from June until the end of August).

We checked explanatory variables for multicollinearity using Variance inflation factor analysis VIF (Zuur *et al.* 2009, 2010). There was no linear correlation between temperature, rainfall and date at either time point evaluated (VIF < 1.37). Visual inspection of residual plots did not reveal obvious deviations from homoscedasticity or normality. All statistical analyses were carried out in R version 3.4.1 (R Core Team 2017). We used R-package lme4 (Bates *et al.* 2015) and lmerTest (Kuznetsova *et al.* 2017) to run the linear mixed effect models. We also calculated marginal (including effect of fixed variables) and conditional (fixed variables and random factors together) R2 values for each of the models function using function r.squaredGLMM from MuMIn package (based on Nakagawa & Schielzeth 2013).

3. Results

The number of captured adult birds was highest in the beginning of the observed period in mid-June and declined towards the end of August in both SDM and LDM groups (Fig. 1a and 1c), while the number of captured young SDM birds was highest in mid-August, and in LDMs approximately a week earlier (early August, Fig. 1b and 1d).

The BRI varied significantly in both adults and young during the breeding season. In adults, two models were within 2 AIC units (Table 2). R^2 of the fixed effects and fixed and random effects together were 0.217 and 0.978, respectively, in the top ranked model (Table 2). After model averaging neither temperature nor rainfall were connected with BRI (Table 4, Supplementary Figs 1–2). Based on the coefficients, BRI showed increase during the breeding season in SDM and LDM males (Figs 2a and 2d; Table 4). In females, the non-linear seasonal pattern (quadratic effect of date) varied between SDMs and LDMs, where BRI first declined during the study period and this decline was faster among LDMs than SDMs. After the decline BRI remained stable in SDMs or slightly increased in LDMs (Figs 2b and 2e; Table 4, Supplementary Figs 3–22).

Among young, two models were within 2 AIC units. However, the top ranked model was clearly simpler than the second best model (Table 3) which thus included uninformative parameters (sensu Arnold 2010). Therefore we only investigated the top ranked model, where R^2 of the fixed effects and fixed and random effects together were 0.196 and 0.981, respectively. There was a weak negative connection between the temperature and BRI, but no correlation between rainfall and BRI (Table 5, Supplementary Figs 1–2). BRI showed a linear increase among SDMs, but according to in-

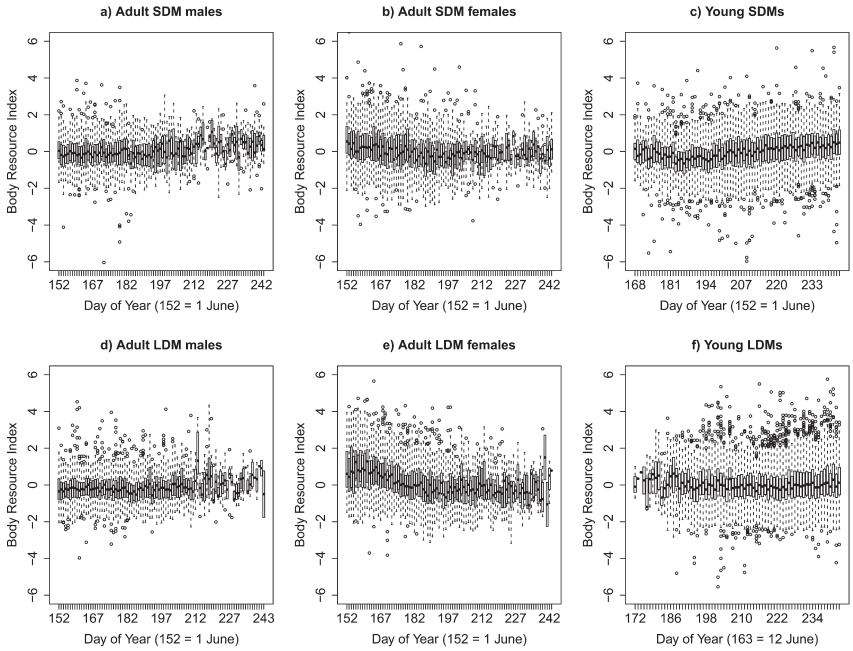

Fig. 2. Connection between BRI and date in (a) SDM (short-distance migrants) males, (b) SDM females, (c) young SDMs, (d) LDM (long-distance migrants) males, (e) LDM females and (f) young LDMs in 20 species in Finland during breeding season (from mid-June till end of August). The box represents the 25–75% limits of the observations and the horizontal black line within the box the median. The whiskers outside the box represent the rest of the observations except the outliers shown in dots. Species-specific graphs are shown in supplementary figures 3–22.

teraction between migratory behaviour and date, this increase was not significant LDMs (Figs 2c and 2f, Table 5, Supplementary Figs 3–22).

4. Discussion

Our findings suggest that there are changes in body condition of songbirds during breeding season, which are linked with sex, age and migratory strategy. Furthermore, we found a weak negative correlation between temperature and body reserves in juvenile birds, however the small coefficient suggests relatively low biological relevance compared with the other explanatory variables.

Among young our findings support the hypothesis that during colder circumstances individuals start to accumulate body reserves to buffer against poor weather conditions (Rogers 1995, Klaassen *et al.* 2004). Lighter body condition during warm periods may be beneficial for predator avoidance (Houston & Mcnamara 1993, Bond & Esler 2006, Esler & Bond 2010) and in reducing the energy required for flight during the busiest feeding period (Freed 1981, Norberg 1981).

On the contrary, we did not find a connection between BRI and temperature in adult birds. Supplementary food experiments have shown that body reserves of breeding females are often resource limited (Schoech 1996) also in small songbirds (Nagy *et al.* 2006, Robb *et al.* 2008). Our findings could indicate that other factors, such as calendar day (e.g., this study) and habitat quality (Johnson 2007), rather than short-term weather variables may influence variation in BRI. Breeding success of females is typically strongly dependent on body reserves determining how many eggs they lay or how many chicks they can feed (Pietiäinen & Kolunen 1993, Eeva *et al.* 2002, Öst *et al.* 2008, Milenkaya *et al.* 2015).

Although we did not find support that rainfall would influence BRI of birds, rainfall levels during brood rearing have been shown to negatively affect both the reproductive output and the sur-

Table 4. Summary statistics of the linear mixed effect model explaining the body reserve index in adult birds after model averaging. Sex is either male or female, Migr is migration behaviour (LDM and SDM, long- and short-distance migrants, respectively), Date is the day of the year, Temp and Rain are the mean temperature and the sum of rainfall during seven days before the trapping of the bird. Statistically significant variables are bolded. Date and weather values were standardized before the analyses.

Variables	*B*	*SE*	*z*-value	*P*
(Intercept)	**0.730**	**0.031**	**23.843**	**< 0.001**
Sex (females compared to males)	**0.003**	**0.000**	**5.644**	**< 0.001**
Migr (LDMs compared to SDMs)	**–0.108**	**0.043**	**2.489**	**0.013**
Date (linear)	**0.294**	**0.075**	**3.042**	**0.002**
Date (quadratic)	0.125	0.100	1.241	0.214
Rain	0.000	0.000	0.186	0.852
Temperature	–0.000	0.000	0.778	0.437
Sex:Migr (LDM females compared to others)	**0.007**	**0.000**	**12.723**	**< 0.001**
Sex:Date (linear) (females compared to males)	**–0.605**	**0.056**	**10.832**	**< 0.001**
Sex:Date (quadratic) (females compared to males)	**0.121**	**0.0508**	**2.379**	**0.017**
Migr:Date (linear) (LDMs compared to SDMs)	0.081	0.106	0.763	0.446
Migr:Date (quadratic) (LDMs compared to SDMs)	0.098	0.143	0.686	0.493
Migr:Rain (LDMs compared to SDMs)	0.000	0.000	0.094	0.925
Migr:Temp (LDMs compared to SDMs)	–0.000	0.000	0.092	0.926
Sex:Rain (females compared to males)	–0.000	0.000	0.182	0.855
Sex:Temp (females compared to males)	0.000	0.000	0.858	0.391
Sex:Migr:Date (linear) (LDM females compared to others)	**–0.624**	**0.071**	**8.766**	**< 0.001**
Sex:Migr:Date (quadratic) (LDM females compared to others)	**0.183**	**0.071**	**2.573**	**0.010**

Table 5. Summary statistics of the top ranked linear mixed effect model explaining the body reserve index in young birds. Migr is migration behaviour (LDM and SDM, long- and short-distance migrants, respectively), Date is day of the year, Temp and Rain are the mean temperature and the sum of rainfall during seven days before the trapping of the bird. Statistically significant variables are bolded. Date and weather values were standardized before the analyses.

Variable	*B*	*SE*	*df*	*t*-value	*P*
(Intercept)	**0.725**	**0.031**	**22**	**23.23**	**< 0.001**
Mig (LDMs compared to SDMs)	**–0.01**	**0.044**	**22**	**–2.26**	**0.034**
Date (linear)	**0.674**	**0.158**	**49**	**4.27**	**< 0.001**
Date (quadratic)	0.163	0.106	33	1.538	0.134
Temp	**0.0005**	**0.0002**	**30270**	**–2.768**	**0.006**
Migr:Date (linear) (LDMs compared to SDMs)	**–0.532**	**0.226**	**51**	**–2.35**	**0.023**
Migr:Date (quadratic) (LDMs compared to SDMs)	0.136	0.155	37	0.88	0.385
Migr:Temp	0.0002	0.0002	38330	1.08	0.281

vival of parents in common buzzards *Buteo buteo* and wheatears *Oenanthe oenanthe* (Lehikoinen *et al.* 2009, Öberg *et al.* 2015). Because the effect sizes of weather variables were relatively small, time of the season was still more important factor explaining changes in BRI of songbirds. This indicates that changes in BRI are linked with seasonal fluctuation depending on sex and age and various life history events. It is unlikely, that the low importance of weather variables would be due to low variability in weather parameters, since temperature and rainfall showed clear variability in the data (from +4.7 to +24.9°C, and from 0 to 119 mm, respectively).

Males showed increasing BRI towards the end of the breeding season, whereas females showed first decline and then slight increase in BRI. This expected result is likely linked to the different life history strategy among sexes. Females need to improve their body condition for egg laying and incu-

bation at the beginning of the breeding season (Suarez *et al.* 2005), which may be why they have highest BRI at that time. Breeding birds, especially females, lose body mass during brood rearing (Hillström 1995, Merilä & Wiggins 1997, Moe *et al.* 2002) and the slope of this loss has been linked with the limitation of resources (Nagy *et al.* 2006). BRI of LDM females showed stronger non-linear U-shape pattern than BRI of SDM females. This is likely due to later breeding dates of the LDMs compared with SDMs (Kluen *et al.* 2017), where decline phase of the LDMs better situated during the study period, whereas the decline among SDMs may have occurred prior the study period.

Males may have low BRI at the beginning of the breeding season when they need to invest in attracting mates and defending territory. To maximize their fitness, males need to acquire as good territory and attract as good quality females as possible (Lozano *et al.* 1996, Hasselquist 1998). In addition, males should guard their females to prevent extra pair copulations, but also at the same time seek their own extra pair copulation opportunities (Møller 1991, Rodrigues 1996, Gil *et al.* 1999). This part of the life cycle occurs typically just before or at the beginning of our study season, which could be the reason for initially low BRI of males. Since males in many species invest less in brood rearing than females (Hemborg 1999) they can start to increase their body reserves towards the end of the breeding season, and thus be more prepared for the autumn migration than females. This can even lead into a situation where adult females are more constrained with time for preparing autumn migration than males. This could be an explanation for why, among some species, adult females migrate later than adult males (Lehikoinen *et al.* 2017).

Opposite to our expectations, the BRI increased faster in young SDMs compared with young LDMs, which are departing earlier for the autumn migration than SDMs (Lehikoinen 2011). LDMs have different migration strategies, but in general, they tend to increase their body reserves towards South Europe before crossing Mediterranean Sea and Sahara desert (Schaub & Jenni 2000). As North European LDM birds do not need to cross large ecological barriers, they can probably start their autumn migration with relatively low body reserves.

5. Conclusions and future perspectives

Our findings highlight that seasonal changes in body condition of songbirds during breeding season are complex and linked with sex and the age of the individuals as well as the day of year, which is likely linked with the life history events of species. We emphasize that our analyses concern individuals whose demographic status is unknown and thus e.g. trapped adults include both breeding and non-breeding birds. To improve our knowledge of seasonal changes in body condition of birds, we encourage conducting more detailed case studies where breeding birds are marked at the beginning of the breeding season, and their breeding attempts are followed. Thus, the impact of the timing of breeding and reproductive success (by marking the nestlings) on changes in body reserves could be studied in more detail. In addition, it would be important to understand what kind of carry-over effects body condition may have especially at the end of the breeding season.

Acknowledgements. The authors wish to express their gratitude to all the volunteer ringers who have participated into the Constant Effort Sites program and collected all the data. A.L. and K.V. received funding from the Academy of Finland (Grants No. 275606 and 283664, respectively).

Varpuslintujen pesimäaikaisen kunnon vaihtelu suhteessa sukupuoleen, muuttostrategiaan ja sääolosuhteisiin

Eläinten kunto ja vararavinnon määrä ovat usein yhteydessä demografisiin muuttujiin kuten pesintämenestykseen ja selviytymiseen. Rajallisessa ravintotilanteessa yksilöiden pitää valita panostavatko ne pesimäkaudella oman kuntonsa ylläpitoon vai lisääntymiseen. Pesimäaikaiseen yksilöiden kuntoon vaikuttavat tekijät tunnetaan edelleen varsin puutteellisesti. Tutkimuksessamme käytimme pitkäaikaista sisämaan seurantapyynnin (SSP) rengastus- ja kontrolliaineistoa selvittääksemme miten sukupuoli, lajin muuttokäyttäytyminen ja sääolosuhteet vaikuttavat yksilöiden kunnon vaihteluun pesimäkauden aikana.

Tarkastelimme kuntoa erikseen nuorilla ja vanhoilla linnuilla käyttäen aineistoa, jossa oli 20 varpuslintulajia ja yhteensä yli 50 000 yksilöä. Yksilön kunto mitattiin painon ja siiven pituuden

suhteena. Olimme erityisesti kiinnostuneita, miten lintuyksilön pyydystämistä edeltävän viikon keskilämpötila ja sadannan summa vaikuttivat kuntoon. Nuorilla linnuilla lämpötila korreloi negatiivisesti kunnon kanssa, mutta vaikutus oli niin heikko, että sen biologinen merkitys lienee vähäinen.

Emme havainneet sääoloilla vaikutusta aikuisten lintujen kuntoon lähi- tai kaukomuuttajilla, eli kokonaisuutena lämpötilan ja sadannan vaikutukset olivat odotettua vähäisempiä. Vanhojen koiraiden kunto parantui pesimäkauden loppua kohden, kun taas vanhojen naaraiden kunto huononi kesäja heinäkuussa. Tämä ero johtuu luultavasti siitä, että naaraiden fysiologinen stressi on pesimäaikana suurempi muninnan ja yleisesti koiraita suuremman pesintään kohdistuvan panostuksen takia. Kunnon laskun takia naaraiden kunto oli koiraita huonompi pesimäkauden lopulla, minkä takia naaraat saattavat olla heikommin valmistuneita tulevaan syysmuuttoon kuin koiraat.

Tuloksemme osoittavat, että pesimäkauden aikana varpuslintujen kunto muuttuu eri suuntiin koirailla ja naarailla, millä voi olla vaikutuksia tulevissa vuodenkierron vaiheissa.

References

Alerstam, T. 1990. Bird migration. — Cambridge University Press.

Arnold, T. W. 2010: Uninformative Parameters and Model Selection Using Akaike's Information Criterion. — The Journal of Wildlife Management 74: 1175–1178.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015: Fitting Linear Mixed-Effects Models Using lme4. — Journal of Statistical Software 12: 1–48.

Bauchinger, U., McWilliams, S. R. & Pinshow, B. 2011: Reduced body mass gain in small passerines during migratory stopover under simulated heat wave conditions. — Comparative Biochemistry and Physiology, Part A 158: 374–381.

Bergmann, C. 1847: Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse. — Göttinger Studien 1: 595–708.

Bond, J. C. & Esler, D. 2006: Nutrient acquisition by female Harlequin Ducks prior to spring migration and reproduction: evidence for body mass optimization. — Canadian Journal of Zoology 84: 1223–1229.

Bradbury, R. B., Wilson, J. D., Moorcroft, D., Morris, A. J. & Perkins, A. J. 2003: Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines. — Ibis 145: 295–306.

Brommer, J. E., Hanski, I. K., Kekkonen, J. & Väisänen, R. A. 2014: Size differentiation in Finnish house sparrows follows Bergmann's rule with evidence of local adaptation. — Journal of Evolutionary Biology 27: 737–747.

Burnham, K. P. & Anderson, D. R. 2002: Model selection and multimodel inference. — Springer, New York, NY.

Castro, G., Myers, J. P. & Ricklefs, R. E. 1992: Ecology and energetics of sanderlings migrating to 4 latitudes. — Ecology 73: 833–844.

Chausson, A., Henry, I., Almasi, B. & Roulin, A. 2014: Barn Owl (*Tyto alba*) breeding biology in relation to breeding season climate. — Journal of Ornithology 155: 273–281.

Duriez, O., Ens, B. J., Choquet, R., Pradel, R. & Klaassen, M. 2012: Comparing the seasonal survival of resident and migratory oystercatchers: carry-over effects of habitat quality and weather conditions. — Oikos 121: 862–873.

Ebbinge, B. S. & Spaans, B. 1995: The importance of body reserves accumulated in spring staging areas in the temperate zone for breeding in dark-bellied brent geese *Branta bernicla* in the high arctic. — Journal of Avian Biology 26: 105–113.

Eeva, T., Lehikoinen, E., Rönkä, M., Lummaa, V. & Currie, D. 2002: Different responses to cold weather in two pied flycatcher populations. — Ecography 25: 705–713.

Esler, D. & Bond, J. C. 2010: Cross-seasonal dynamics in body mass of male Harlequin Ducks: a strategy for meeting costs of reproduction. — Canadian Journal of Zoology 88: 224–230.

Freed, L. A. 1981: Loss of mass in breeding wrens: stress or adaptation? — Ecology 62: 1179–1186.

Fujii, S., Hironaka, M. & Nomakuchi, S. 2005: Male body size and brooding success under natural conditions in the freshwater Japanese goby *Rhinogobius* sp. OR (orange type). — Journal of Ethology 23: 127–132.

Gaillard, J., Sempéré, A. J., Boutin, J., Van Laere, G. & Boisaubert, B. 1992: Effects of age and body-weight on the proportion of females breeding in a population of Roe Deer (*Capreolus capreolus*). — Canadian Journal of Zoology 70: 1541–1545.

Gil, D., Graves, J. A. & Slater, P. J. 1999: Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. — Animal Behavior 58: 995–1000.

Gruar, D., Peach, W. & Taylor, R. 2003: Summer diet and body condition of Song Thrushes *Turdus philomelos* in stable and declining farmland populations. — Ibis 145: 637–649.

Hamer, K. C., Monachan, P., Uttley, J. D., Walton, P. & Burns, M. D. 1993: The influence of food-supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. — Ibis 135: 255–263.

Hasselquist, D. 1998: Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. — Ecology 79: 2376–2390.

Hemborg, C. 1999: Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers *Ficedula hypoleuca.* — Journal of Animal Ecology 68: 429–436.

Hillström, L. 1995: Body mass reduction during reproduction in the pied flycatcher *Ficedula hypoleuca*: physiological stress or adaptation for lowered cost of locomotion? — Functional Ecology 9: 807–817.

Houston, A. I. & Mcnamara, J. M. 1993: A theoretical investigation of the fat reserves and mortality levels of small birds in winter. — Ornis Scandinavica 24: 205–219.

Jacobs, A. C., Reader, L. L. & Fair, J. M. 2013: What determines the rates of double brooding in the Western Bluebirds? — The Condor 115: 386–393.

Johnson, M. D. 2007: Measuring habitat quality: A review. — The Condor 109: 489–504.

Klaassen, M., Oltrogge, M. & Trost, L. 2004: Basal metabolic rate, food intake, and body mass in cold-warm-acclimated Garden Warblers. — Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 137: 639–647.

Kluen, E., Nousiainen, R. & Lehikoinen, A. 2017: Breeding phenological response to weather conditions in common Finnish birds: resident species respond stronger than migratory species. — Journal of Avian Biology 48: 611–619.

Kostrzewa, A. & Kostrzewa, R. 1990: The relationship of spring and summer weather with density and breeding performance of the buzzard Buteo buteo, goshawks Accipiter gentilis and kestrel *Falco tinnunculus*. — Ibis 132: 550–559.

Krams, I., Cīrule, D., Vrublevska, J., Nord, A., Rantala, M. J. & Krama, T. 2013: Nocturnal loss of body reserves reveals high survival risk for subordinate great tits wintering at extreme low ambient temperatures. — Oecologia 172: 339–346.

Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. B. 2017: lmerTest Package: Tests in Linear Mixed Effects Models. — Journal of Statistical Software 82: 1–26.

Lehikoinen, A. 2011: Advanced autumn migration of sparrowhawk has increased the predation risk of long-distance migrants in Finland. — PLoS One 6: e20001.

Lehikoinen, A., Byholm, P., Ranta, E., Saurola, P., Valkama, J., Korpimäki, E., Pietiäinen, H. & Henttonen, H. 2009: Reproduction of common buzzard at its northern range margin under climate change. — Oikos 118: 829–836.

Lehikoinen, A., Santaharju, J. & Møller, A. P. 2017: Sex-specific timing of autumn migration in birds: impact of sexual size dimorphism and differences in breeding investment. — Ornis Fennica 954: 53–65.

Lindström, K. 1998: Energetic constraints on mating performance in the sand goby. — Behavioral Ecology 9: 297–300.

Lozano, G. A., Perreault, S. & Lemon, R. E. 1996: Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla.* — Journal of Avian Biology 27: 164–170.

Ludwig, G. X., Alatalo, R. V., Helle, P., Lindén, H., Lindström, J. & Siitari, H. 2006. Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. — Proceedings of the Royal Society London Biological series 273: 2009–2016.

Macleod, R., Barnett, P., Clark, J. A. & Cresswell, W. 2005: Body mass change strategies in blackbirds *Turdus merula*: the starvation-predation risk trade-off. — Journal of Animal Ecology 74: 292–302.

Meller, K., Vähätalo, A. V., Hokkanen, T., Rintala, J., Piha, M. & Lehikoinen, A. 2016: Interannual variation and long-term trends in proportions of resident individuals in partially migratory birds. — Journal of Animal Ecology 85: 570–580.

Merilä, J. & Wiggins, D. A. 1997: Mass loss in breeding blue tits: The role of energetic stress. — Journal of Animal Ecology 66: 452–460.Mills, A. M. 2005: Protogyny in autumn migration: Do male birds "play chicken"? — The Auk 122: 71–81.

Milenkaya, O., Catlin, D. H., Legge, S. & Walters, J. R. 2015: Body condition indices predict reproductive success but not survival in a sedentary, tropical bird. — PLoS ONE 10: e0136582.

Mitchell, G. W., Wheelwright, N. T., Guglielmo, C. G. & Norris, R. D. 2012: Short- and long-term costs of reproduction in a migratory songbird. — Ibis 154: 325–337.

Moe, B., Langseth, I., Fyhn, M., Gabrielsen, G. W. & Bech, C. 2002: Changes in body condition in breeding kittiwakes *Rissa tridactyla*. — Journal of Avian Biology 33: 225–234.

Møller, A. P. 1991: Why mated songbirds sing so much – mate guarding and male announcement of mate fertility status. — American Naturalist 138: 994–1014.

Møller, A. P. 2013: Long-term trends in wind speed, insect abundance and ecology of an insectivorous bird. — Ecosphere 4(1): 1–11.

Morrison, R. I. G., Davidson, N. C. & Wilson, J. R. 2007: Survival of the fattest: body stores on migration and survival in red knots *Calidris canutus islandica*. — Journal of Avian Biology 38: 479–487.

Nakagawa, S. & Schielzeth, H. 2013: A general and simple method for obtaining R^2 from generalized linear mixed-effects models. — Methods in Ecology and Evolution 4: 133–142.

Nagy, L., Stanculescu, D. & Holmes, R. T. 2006: Mass loss by breeding female songbirds: food supplementation supports the energetic stress hypothesis in black-throated blue warblers. — Condor 109: 304–311.

Newton, I. 2008: The migration ecology of birds. — Academic Press.

Norberg, A. 1981: Temporary mass decrease in breeding birds may result in more fledged young. — American Naturalist 118: 838–850.

Öberg, M., Arlt, D., Pärt, T., Laugen, A. T., Eggers, S. &

Low, M. 2015: Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. — Ecology and Evolution 5: 345–356.

Ormerod, S. J. & Tyler, S. J. 1990: Assessments of body condition in dippers *Cinclus cinclus*: potential pitfalls in the derivation and use of condition indices based on body proportions. — Ringing and Migration 11: 31–41.

Öst, M., Ydenberg, R., Lindström, K. & Kilpi, M. 2003: Body condition and the grouping behavior of brood-caring female common eiders (*Somateria mollissima*). — Behavioural Ecology and Sociobiology 54: 451–457.

Öst, M., Smith, B. D. & Kilpi, M. 2008: Social and maternal factors affecting duckling survival in eiders *Somateria mollissima*. — Journal of Animal Ecology 77: 315–325.

Pearce-Higgins, J. W., Eglington, S. M., Martay, B. & Chamberlain, D. E. 2015: Drivers of climate change impacts on bird communities. — Journal of Animal Ecology 85: 943–954.

Pérez, J. H., Krause, J. S., Chmura, H. E., Bowman, S., McGuigan, M., Asmus, A. L., Meddle, S. L., Hunt, K. E., Gough, L., Boelman, N. T. & Wingfield, J. C. 2016: Nestling growth rates in relation to food abundance and weather in the Arctic. — The Auk 133: 261–272.

Pietiäinen, H. & Kolunen, H. 1993: Female body condition and breeding of the Ural owl *Strix uralensis*. — Functional Ecology 7: 726–735.

Piha, M. 2014: Constant Effort Sites in Finland: Population and productivity indices 1987–2013 (in Finnish with English summary). — Linnut-vuosikirja 18: 108–115.

R Core Team 2017: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria. URL https://cran.r-project.org/

Robb, G. N., McDonald, R. A., Chamberlain, D. E. & Bearhop, S. 2008: Food for thought: supplementary feeding as a driver of ecological change in avian populations. — Ecology and the Environment 6: 476–484.

Rodrigues, M. 1996: Song activity in the chiffchaff: Territorial defence or mate guarding. — Animal Behaviour 51: 709–716.

Rogers, C. M. 1995: Experimental evidence for temperature-dependent winter lipid storage in the dark-eye junco (*Junco hyemalis oreganus*) and song sparrow (*Melospiza melodia morphna*). — Physiological Zoology 68: 277–289.

Schaub, M. & Jenni, L. 2000: Body mass of six long-distance migrant passerine species along the autumn migration route. — Journal of Ornithology 141: 441–460.

Schoech, S. J. 1996: The effect of supplementary food on body condition and the timing of reproduction in a cooperative breeder, the Florida scrub-jay. — Condor 98: 234–244.

Smith, D. W. & Jenkins, S. H. 1997: Seasonal change in body mass and size of tail of northern beavers. — Journal of Mammalogy. 78: 869–876.

Suarez, F., Traba, J. & Herranz, J. 2005: Body mass changes in female tawny pipits*Anthus campestris* during the nesting stage. — Journal of Ornithology 146: 372–376.

Svensson, L. 1992: Identification Guide to European Passerines. 4th edition.

Valkama, J., Saurola, P., Lehikoinen, A., Lehikoinen, E., Piha, M., Sola, P. & Velmala, W. 2014: Suomen rengastusatlas. Osa II. — Luonnontieteellinen keskusmuseo ja ympäristöministeriö, Helsinki.

Van Horne, B., Olson, G. S., Schooley, R. L., Corn, J. G. & Burnham, K. P. 1997: Effect of drought and prolonged winter on Townsend's ground squirrel demongraphy in shrubsteppe habitats. — Ecological Monographs. 67: 295–315.

Venäläinen, A., Tuomenvirta, H., Pirinen, P. & Drebs, A. 2005: A Basic Finnish Climate Data Set 1961–2000. — Description and Illustrations.

Vernasco, B. J., Sillett, T. S., Marra P. P. & Ryder, T. B. 2018: Environmental predictors of nestling condition, postfledging movement, and postfledging survival in a migratory songbird, the Wood Thrush (*Hylocichla mustelina*). — The Auk 135: 15–24.

Zaniewicz, G., Meissner, W. & Ozarowska, A. 2018: Estimation of fat reserves of Robins (*Erithacus rubecula*) migrating through the southern coast of the Baltic Sea in spring. — Ornis Fennica 95: 41–47.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A. & Smith, G. M. 2009: Mixed effects models and extensions in ecology with R, 1st edition. — Springer, New York.

Zuur, A. F., Ieno, E. N. & Elphick, C. S. 2010: A protocol for data exploration to avoid common statistical problems. — Methods in Ecology and Evolution 1: 3–14.

Online supplementary material

Figure S1. Connection between body reserve index (BRI) and temperature in 20 species.
Figure S2. Connection between body reserve index (BRI) and rainfall in 20 species.
Figures S3–22. Species-specific figures showing Reserve Index in relation to day of year among males, females and young birds in 20 species.